STUDIES IN THE AUSTRALIAN ACACIAS. VI.

THE MERISTEMATIC ACTIVITY OF THE FLORAL APEX OF ACACIA LONGIFOLIA AND
ACACIA SUAVEOLENS AS A HISTOGENETIC STUDY OF THE ONTOGENY OF THE CARPEL.

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(Plates ii–v; fifteen Text-figures.)

Introduction.

Taking its origin in Goethe's (1790) "Versuch die Metamorphose der Pflanzen zu erklären", and regarded by Robert Brown (1840, p. 108) as generally accepted, the classical theory that the carpel is a modified leaf has held sway for more than a hundred years. In recent times criticisms ranging from modification to complete negation of the theory have arisen. So much speculation and assumption and criticism (of such speculations and assumptions) have been written about this subject, that the only excuse for adding to the literature is that there are new relevant facts to be recorded. In spite of frequent reference to the need for considering primordial stages and the ontogeny of the carpel, the literature shows few illustrations of these features, particularly of cellular details of the meristematic tissues concerned. In this paper I will describe and illustrate the origin of the floral organs in two species of *Acacia*, showing the relation of their primordial tissues to the tissues of the floral axis. The central interest will lie in finding the relation of the carpel primordium to the apex of the flower and in comparing its mode of origin with that of the other parts of the flower.

The two species, *Acacia longifolia* Willd. and *Acacia suaveolens* Willd., were given by Saunders (1929, pp. 225–7) as illustrations of the theory of Carpel Polymorphism (1925, etc.). I undertook an examination of them to test the objections to the theory based on the examination of *Acacia Baileyana* (Newman, 1933 and 1934). As the work progressed it became clear that important evidence was here available concerning other criticisms of the old theory of the carpel that were being raised by McLean Thompson (1929, 1931, 1932, 1934), Hamshaw Thomas (1931, 1934) and Victor Grégoire (1931). In none of the papers mentioned do the four authors support their theories by illustrating the cellular details of the ontogeny of the carpel and its relation to the apical meristems of the floral axis; and this is the type of evidence that will be presented in the following pages.

MATERIAL AND METHODS.
DESCRIPTION OF RELEVANT FEATURES OF THE SPECIES.
Acacia longifolia.

The flowers of *Acacia longifolia* are in cylindrical spikes. In the bud stage the only restriction is due to the tight packing of the young flowers on the axis

of the spike. There is no marked distortion of the flowers. Each flower is in the axil of a bract which overlaps the bract of the flower next above so that in the very young condition the surface of the spike consists of the tips of the subtending bracts. The only distortion is that the flowers are elongated or flattened in the direction of their axis. The construction of this inflorescence makes it easy to orientate the material for sectioning, and to determine in microscopic examination how a flower lies with regard to the axis of the spike. There are four sepals and four petals. The stamens number approximately between 90 and 110. The single legume has ten or twelve ovules, in the young state is relatively small, and in the pod stage long, narrow and almost cylindrical. In rare cases, more than one legume has been seen in a flower; but the disposition of the sections was not such as to disclose the relationship of the legumes to one another or to the axis of the flower. The orientation of the legume to the axis of the spike appears to have no constancy. The foliage is of the phyllodineous type, with flat phyllodes having several parallel "nerves".

Acacia suaveolens.

The flowers of *Acacia suaveolens* are in globular heads borne in axillary racemes. The young racemes are enclosed in several large imbricate bracts, and the flower heads are subtended by bracts. In the bud these bracts so tightly clasp the young inflorescence and flower-heads that there is often a considerable distortion of the young flowers (Text-fig. 11). The bracts are deciduous at anthesis. There are no bracts subtending the individual flowers. Such an arrangement makes it impossible to orientate the material in sectioning, and often difficult to determine in microscopic examination how a flower lies with regard to the axis of the flower-head. There are five sepals and five petals, though sometimes six or four are found. The stamens number approximately between 60 and 80. The single legume has five or six ovules, in the young state is relatively massive, and in the pod stage flat, broad and short. The foliage is of the phyllodineous type, with flat phyllodes having one "nerve".

MANIPULATION OF THE MATERIAL.

All the material was fixed in a formalin–alcohol solution (50 c.c. absol. ethyl alcohol, 50 c.c. water, 6 c.c. commercial formalin). In the case of *A. suaveolens*, it was found necessary to dissect out as many bracts as possible. In the case of *A. longifolia* the young spikes were rolled and squeezed between the fingers and cut longitudinally, either down the middle of the axis or twice parallel with the axis. All material was thoroughly exhausted when put into the fixing fluid. After dehydration and clearing in either xylol or cedar-wood oil, the material was embedded in paraffin.

Serial sections were cut with a microtome, mostly at a thickness of 6μ ($0\cdot006$ mm.), a few being cut at 4μ and 8μ. The block was usually cooled with ice and salt. This material was very hard, probably on account of the hardening of the tannin in the cells by the fixative. The consequent friction during cutting invariably generated static electricity that caused disruption of the ribbon as it left the edge of the knife. This was overcome by producing a high-frequency brush discharge around the material and knife (Batson, 1920, describes the method). The stain used, except where specified, was a triple stain comprising Safranin in 50% alcohol differentiated with $0\cdot005\%$ Light Green in 95% alcohol, a saturated solution of Orange G in clove oil and a saturated solution of Light

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Green in clove oil. Immersion of the slides in water after the alcoholic safranin makes the final differentiation of the safranin much easier. There is no use in giving a schedule, because the times vary with both species and stage of development.

EXAMINATION OF THE MATERIAL.

The necessary details of the photography and drawing, together with the standardized annotations, are given in the "Notes on the Illustrations" (p. 85).

The first attempt to find the relation of the primordium of the legume to the apex of the flower was by means of scale models made of plasticene (modelling material). The models were made at a magnification of approximately 375 from series of sections 0·006 mm. thick. Sheets of plasticene were rolled to a thickness of 2·25 mm. (0·006 × 375), and on them were drawn, with the aid of the camera lucida, the outlines of the component sections of series through young flowers. The outlines being cut out and superposed in order, scale models of young flowers were built up.* Models were made of the portion above the sepals at different stages of development. After smoothing the surface and cutting off the petals level with the base of the outer stamens (except in Plate v, fig. 51) and cutting off some or all of the stamens, the models appeared as in Plate v, figures 51–59. They represent two critical stages from *Acacia longifolia* (58–59) and a complete series of stages from *Acacia suaveolens*. The additional stages for *longifolia* are represented by outline drawings (Text-figs. 1–5).

DESCRIPTION OF THE EVIDENCE.
METHOD OF APPROACH.

In this description I will not use terms whose morphological or spatial significance could assume an interpretation of the legume or the carpel. The term "carpel" assumes an interpretation of the legume, the terms "legume" and "apex" (of the flower) have a spatial significance in the problem; therefore they will not be used.

In the succeeding section of the paper the evidence will be interpreted against the background of knowledge of the vegetative growing point found in recent literature. In the final section the criticisms of the classical theory will be discussed and an attempt made at a constructive contribution to the morphology of the carpel.

THE EVIDENCE.
External appearances.

The young floral axis is approximately cylindrical, with its upper portion nearly hemispherical. The appearance, from (and including) the insertion of the petals upwards at the time of the petal primordia,† is shown by a model of *suaveolens* (Plate v, fig. 51) and an outline of a section of a young flower with bract of *longifolia* (Text-fig. 1). Soon after this stage the outer part of the convex end of the axis develops into a "shoulder" leaving a central convex area, which I will call the "dome". On the "shoulder" the stamen primordia arise, beginning at its edge and in front of the sepals (not shown in the models) (Plate v, fig. 52 for *suaveolens* and Text-fig. 2 and Plate v, fig. 59 for *longifolia*).

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* Zimmermann (1928, p. 299) made a model by drawing on and cutting out cardboard, adding paraffin to the appropriate thickness, and sticking together the magnified sections thus made.

† See p. 67 for terminology.

The area of the "shoulder" becomes filled with the primordia of the stamens during whose early growth the dome becomes higher (Plate v, figs. 53–5 for *suaveolens* and Plate v, fig. 59 and Text-fig. 3 for *longifolia*). The next development appears to occur at a younger stage of staminal growth in *longifolia* than in *suaveolens*, i.e., the stage of Plate v, figure 55 is omitted in *longifolia*. The regular contour of the dome is obliterated by an ex-centric development that appears to affect about half—possibly more—of the circumference of its transverse projection, but does not extend across its vertical centre. The excrescence so formed has a crescent shape in vertical projection. This stage is represented for *suaveolens* by a model (Plate v, fig. 56) and for *longifolia* by the outline of a section at a slightly older stage (Text-fig. 4). During this development the surface of the dome develops a steeper slope. The crescentic excrescence continues its vertical growth (Plate v, figs. 57–8 and Text-fig. 5) and, above its insertion on the dome, extends its arms forward in parallel growth so that a definite groove is formed between them. The margins of this groove, by increase in thickness and slight curvature of the arms, are brought into close association. Having an idea of the "solid" appearance of the development of the flower to this stage, we can turn to the changes in the tissues, of which this is the outward appearance.

Internal Development of Tissues.

In *longifolia* it will be easy to trace the enlargement of the young developing flower, for, though it is closely shut in between its own bract and those of adjacent flowers, there is no great distortion of its shape. But in *suaveolens* the difficulty of determining the orientation of the section and the frequent, marked distortion (cf. Text-fig. 11 and Plate v, figs. 66–8) prevent a comparison of sizes in the younger stages. For the sepals, petals, and stamens, the description will not be carried further than the formation of the primordia.*

At the time the sepal initials are formed, the axis is about 0·125 mm. long in both species, and its breadth is approximately 0·075 mm. in *longifolia* and 0·1 mm. in *suaveolens*. The upper surface of the axis is convex, the degree of curvature varying considerably in *suaveolens* on account of the distortion. The three outer layers of cells appear to have been formed with regularity by anticlinal division walls which are generally straight. They have very large nuclei in proportion to their size, and the cytoplasm is very dense, with very little vacuolation, if any. Beneath these layers are from one to three layers in which the direction of division is at random, the nuclei are relatively small and the cytoplasm is increasingly vacuolated the further the cell is from the surface. This zone merges into the pith of large, much vacuolated cells with small nuclei. The walls of the vacuolating and vacuolated cells are curved.

In Plate ii, figure 1, of *longifolia*, the sepal primordia consist of a fold in the outer layer (increase by divisions with anticlinal wall formation) under which are cells, continuous with the second layer and some at least of which have been formed by divisions with periclinal walls. In the younger stage of *suaveolens*, shown in Plate iii, figure 19, the initial of the sepal is seen clearly as a fold in the outer layer under which divisions with periclinal walls have occurred in the second layer. There may be some contribution from the third layer.

The description of the formation of the petal initials would be a repetition of that given above for the sepal initials, except for relative differences in age of the initials illustrated. This stage is shown in Plate ii, figure 2 for *longifolia*.

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* See p. 67 for terminology.
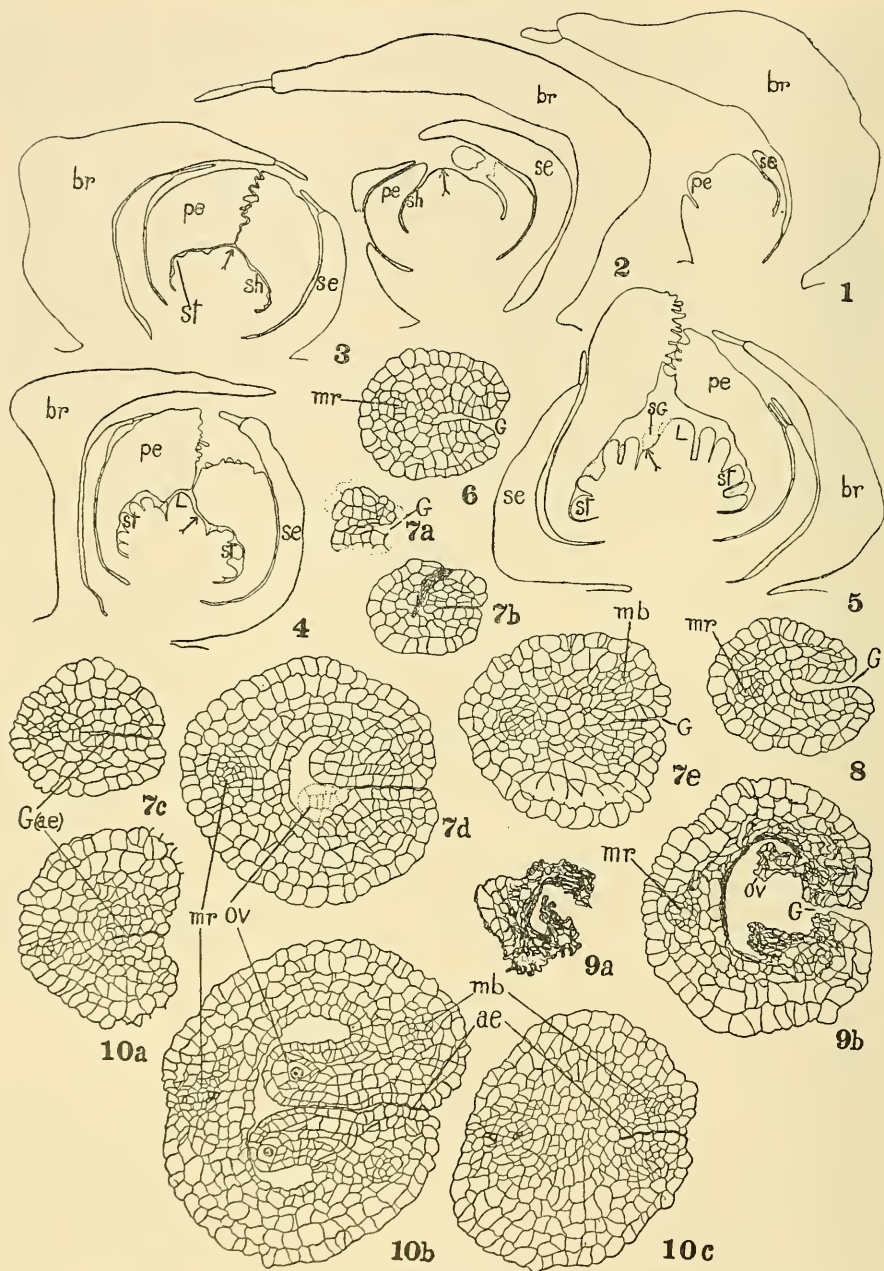
Text-figures 1-10c.—*Acacia longifolia.* Magnification, × 80 for Figures 1-5, and × 160 for Figures 6-10c.

1-5.—Longitudinal sections of young flowers corresponding respectively with the models of *Acacia suaveolens* shown in Plate v, figures 51, 52, 54, (older than) 56 and 57. Note the hairs on the bracts, sepals and petals. The stages shown are: petal primordia (1), the "shoulder" (*sh*) before stamens (2), the stamen initials (3), the lateral ovule-

In the left-hand initial some of the cells appear to have been formed from the second layer by divisions with walls anticlinal to the *inclined* surface of the fold. Plate iii, figure 20 shows the petal initial in *suaveolens*. About this time the cells of the pith become greatly enlarged and begin to deposit globules of an unidentified substance which stains heavily with safranin and haematoxylin.

Examples of the distortion of the young developing flower of *suaveolens* are shown in Plate v, figures 66–68, in which the three zones of cell layers, based on nuclear and cytoplasmic conditions and direction of wall formation, can be clearly observed. These are at a later stage than that just described.

Still maintaining the three zones of tissue, the axis has about doubled its height above the level of insertion of the petal initials before they have made much growth. During the stages to be described in this paragraph the petals of *longifolia* become considerably larger than those of *suaveolens*. As the petals enlarge, divisions with periclinal walls begin to occur just above them in the second layer of the axis (Plate ii, fig. 3 and Plate iii, fig. 21). These divisions extend (Plate ii, fig. 4 and Plate iii, fig. 22) from the petals for about one-third of the distance over the convex upper surface of the axis (Plate ii, fig. 5 and Plate iii, fig. 23). In this way the shoulder is formed and the central dome is differentiated. The second layer of the dome is continuous with the second and third layers of the shoulder, and the third layer of the dome is continuous with the fourth layer of the shoulder (originally third layer of the axis). This fourth layer of the shoulder is becoming vacuolated and losing the regular shape of its cells.

In *suaveolens*, the last stage of shoulder formation is concurrent with the beginning of stamen formation. The stamen initials are formed on the shoulder and, except that the number of cells concerned in each initial is very much smaller, the same description applies to them as to the initials of the sepals and petals. A fold in the outer layer of the shoulder of the axis has, underneath it, cells derived from the second layer by periclinal wall-formation, some possibly by divisions in a fold of the second layer with walls anticlinal to the inclined surface of the fold (Plate ii, figs. 6–8, and Plate iii, figs. 23–26).

By the time the stamen initials have developed into primordia about four cells high, complete vacuolation has extended in the axis to the second or third layer of cells in the shoulder, i.e., to layers continuous with the second layer of the central dome. In the central dome itself there are still three layers of cells

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bearing organ (4) and the formation of the groove (5). Note the interlocking of the tips of the petals in 3. Compare these figures respectively with Plate ii, figures 2, 5, 7, 14 and 18.

6.—Transverse section, 0·1 mm. from the base of young organ, 0·18 mm. long before formation of the ovules.

7a-e.—Representing a series of 55 transverse sections of an ovule-bearing organ with primordia of the ovules. Sections are 6μ, the numbers represented being 2, 6, 11, 38 and 50, beginning from the tip. Tissue is crushed in one part of *b*. Note the continuation of the groove to the tip of the organ, and the ovules arising at the edges of the incurved arms of the groove.

8.—Transverse section about half-way up a sterile ovule-bearing organ from a flower of the same staminal development as that of Text-figures 7a-e.

9a, b.—Transverse sections from the base of the style and in the region of ovules in an organ whose ovules had attained about the development of those in Text-figures 10a-c before sterility set in.

10a-c.—Transverse sections of an ovule-bearing organ through the base of the style, middle pair of ovules and just below the loculus, at the stage of the mother cell. Compare *b* with Plate v, figure 76.

with non-vacuolated cytoplasm and large nuclei. Under these are one or two layers of intermediate vacuolation. The dome projects further than before and the cells of its second and third layers appear to have increased in length vertically to the surface with a slight distortion whereby the direction of their long axis approaches that of the axis of the flower. The maximum height attained by the dome is only about the thickness of the three outer layers of cells—between 0·025 and 0·03 mm. In both species there may be variations in the shape of the dome. In *suaveolens* they are derived from the general distortion of the young flower, already described (Plate iii, figs. 25–27). In *longifolia* the presence of the bract causes the petals to be pressed down on the growing axis, whereby some distortion of the dome occurs (Plate ii, figs. 7–8). The development of the dome appears to be due more to increase in cell size than to cell division; for the number of cells in each of the two outer rows is between about 15 and 18 before and after the increase (cf. Plate ii, fig. 6 with fig. 8, and Plate iii, fig. 24 with fig. 27). The diameter of the base of the dome shows almost no increase at this stage.

The next stage of development shows a fold in the outer layer of cells of the dome, occupying less than half of the outline of the dome in vertical section, and placed to one side of the vertical centre. The space beneath the fold is filled with cells derived from the second layer mostly by walls that appear to be periclinal (Plate ii, figs. 9–12 for *longifolia* and Plate iii, figs. 28–30 for *suaveolens*). This corresponds with the stage shown in Plate v, fig. 56. The radius of curvature of the central dome is much smaller than that of the young axis during the formation of the sepal, petal and stamen initials; and the cells of the second and third layers are elongated vertically in the central dome in contrast to those of the young axis. Remembering these differences, there is no fundamental divergence of the process just described from the mode of formation of the initials of the sepals, petals and stamens. The initial described last develops into the ovule-bearing organ.

If the foregoing description is true, *the mode of formation of the initials of each of the organs of these flowers is essentially the same.* The differences that exist are mainly concerned with the area of the surface of the axis that is involved, and the radius of the axis at the level concerned.

An examination of Plate ii, figures 3–8, and Plate iii, figures 21–27, shows that the dome first existed as the residue of the convex upper surface of the axis after the shoulder had been formed. Its increase in size (height) was by increase in size and negligible increase in number of cells. Its three outer layers of cells were continuous with the three outer layers of cells of the rest of the axis (before shoulder formation) and have the same protoplasmic characteristics. Its origin is in no way comparable with the origin of the initials of the floral organs below it; it is merely a part of the axis slightly extended by cell enlargement. The initial of the ovule-bearing organ having been formed, there remains a part of the dome not involved, and represented in median vertical section by a region having 8–10 cells in the outer layer (slightly more than half the number of cells in the original, full contour). With the formation of the last initial, the slope of the residual portion of the dome becomes steeper. If the axis of symmetry of the axial tissues of the young flower be followed to the upper surface, it will be seen to emerge in the centre of the dome; but after the formation of the last initial, there is an appearance as if this axis were bent away from the initial. The "flow" of cells from the apex of the large-celled pith

emerges on the surface at about the seventh or eighth cell of the surface layer (in median L.S.) from the base of the dome opposite the initial, that is, at the original centre of the surface of the dome. This point is now slightly displaced by the formation of the initial of the ovule-bearing organ (cf. Plate ii, figs. 6–8 with figs. 9–12 for *longifolia*, and Plate iii, figs. 24–27 with figs. 28–30 for *suaveolens*, remembering the distortions).

The course of development of the sepals, petals and stamens beyond the formation of their primordia is not followed in this paper. The story of the residue of the dome is described below (p. 65). The development of the ovule-bearing organ will now be described to the stage where its general form and the manner of bearing ovules are clearly displayed.

When the initial of the ovule-bearing organ has developed into a primordium of four or six cells in height and six cells in thickness (Plate ii, figs. 13–14 for *longifolia*, and Plate iii, figs. 31–32 for *suaveolens*), the cells are densely cytoplasmic and have relatively large nuclei, as in the three outer layers of the axis in the previous stages. Passing down through the position of the original second and third layers of the dome, the cells have an increasing degree of vacuolation, an increase of size and relatively small nuclei. The large, irregular pith cells now extend to where was the centre of the base of the dome. To either side of this point there is a distinct difference in the organization of the cells. Those on the side towards the primordium are larger and slightly vacuolate, compared with those in the residue of the dome, except that a couple of vertical rows towards the centre of the base have retained the feature of relatively large nuclei. The residue of the dome has retained till now the disposition and appearance of its three (outer) layers; but there is a beginning of change with slight vacuolation. The increase in size of the cells on the side towards the primordium is accompanied by an orientation of their length, such that there is an appearance of a flow of tissue obliquely from one side of the tip of the pith into the primordium. The residue of the dome has the appearance of having been tilted about the outer edge of its base as a pivot by the increase in size of these cells.

It must be remembered that, on account of the small dimensions of the dome, if the fold that was the initial of the ovule-bearing organ were relatively long, it would be very much curved in the horizontal plane. When such an initial grows out as the primordium, it must assume a grooved form, opening towards the space above the residue of the dome. This feature is shown in the solid by Plate v, figure 58 for *longifolia*, and Plate v, figures 56–57 for *suaveolens*. In *longifolia* the approximation and final contact of the two arms of the grooved primordium occurs much more rapidly than in *suaveolens*; so that, whereas in some stages a section down the groove of *longifolia* will inevitably show one or other of the approximating surfaces, one or two sections can be cut down the groove of *suaveolens* without including either surface. It will be noticed also at this stage that, with the close crowding of the stamens, the space available for the longitudinal growth of the ovule-bearing organ causes it to grow in the vertical direction, and brings the arms of the groove down on to the upper part of the residue of the dome.

Stages in the development of the groove are illustrated in Plate ii, figures 15–18 for *longifolia*, and Plate iv, figures 33a–37 for *suaveolens*. During this development: (1) the region of complete vacuolation and irregular cells, i.e., the pith, extends in the residue of the dome to level of formation of the initial of the ovule-bearing organ; and (2) in the base of the primordium, vacuolation

of the cytoplasm and the decrease in the nucleus/cell size-ratio has left a small central longitudinal zone of cells almost unaffected (Plate ii, fig. 16 for *longifolia*, and Plate iv, fig. 35 for *suaveolens*). Dense cytoplasm and relatively large nuclei are still maintained at the tip and on the arms of the organ. The aspect of these features as seen in transverse section is shown in the series of sections illustrated in Plate iv, figures 39*a–f* (cf. Plate ii, fig. 14), and Plate iv, figures 38*a–f* (cf. Plate iv, figs. 34*a–b*), for *longifolia* and *suaveolens* respectively. In each case the section shown in *d* passes through the upper part of the residue of the dome whose smaller cells can be seen on the right. Plate ii, figure 18, and Plate iv, figure 37, show a further stage in both species with a similar distribution of cellular differences as before, except that marked vacuolation and the reduction of the nucleus/cell size-ratio has now affected all of the residue of the dome, in some of whose outer cells there is a deposition of the globules that stain deeply with safranin and haematoxylin. The arms of the primordium of the ovule-bearing organ now extend over, and make contact with the upper surface of the residue of the dome. Their extent in the transverse plane is already much greater than when the initial was formed.

Neglecting the residue of the dome, we will follow further the development of the ovule-bearing organ. It extends at the stage shown in Plate ii, figure 18, and Plate iv, figure 37, about 0·09 mm. and 0·125 mm. respectively above the insertion of the adjacent stamens. Text-figures 6 (*longifolia*) and 12 (*suaveolens*) show transverse sections of the organ about half-way up when the heights are 0·18 mm. and 0·16 mm. respectively, the arms of the groove being now almost in contact. Further growth is such that the rate of increase is greater on the outside of the arms than on the sides nearly in contact. Consequent upon this, the margins of the grooved organ remain in contact and a central cavity is formed. Into this cavity the ovules arise as outgrowths from the margins of the groove. The two series of sections shown in Text-figures 7*a–e* for *longifolia* and 13*a–g* for *suaveolens* illustrate this point and show that the groove extends to the very tip of the organ and below the insertion of the ovules. The part of the adult organ that is extended for some distance above the ovuliferous region is a prolongation of the tip, though in passing upwards the grooved condition is soon lost. Sections made just above, at the middle of, and just below the ovuliferous region, at the stage of the megaspore mother cell, are illustrated for both species in Text-figures 10*a–c* and 15*a–c*. In both these last stages the appressed epidermes of the margins are clearly discernible on the right of the organ and the midrib on the left.

Four photomicrographs are submitted in confirmation of these drawings concerning the appressed epidermes. Plate v, figure 70, is of a longitudinal section through the margins of the organ when it is about 0·25 mm. long in *longifolia*. Plate v, figure 69*a*, is a similar photomicrograph for the organ when it is about 0·225 mm. long in *suaveolens*. Plate v, figure 77, is of a section (at the base of the ovuliferous region) in the series from which Text-figure 15 is taken, the line of the two appressed epidermes being clearly visible on the right side of the structure. Plate v, figure 76, is of the same section as Text-figure 10*b* and is a clear confirmation of the drawing. An interesting confirmation of the single curved structure of the ovule-bearing organ is derived from cases of sterility. In the flower from which Text-figure 8 was taken, the stamens were at the stage of those in the flower from which Text-figures 7*a–e* were taken. Text-figures 9*a–b* show degeneration that had set in about the stage of Text-

figures 10*a–c* or a little earlier. Text-figure 14 is of *suaveolens* where sterility had set in before formation of the ovules (with degeneration). Occasionally the organ does not have the margins closed together, in which case the ovules are visible, as shown in Plate v, figure 69*b*, of *suaveolens* (length a little more than 0·25 mm.).

The single curved structure of the ovule-bearing organ can still be discerned at the time of fertilization. Plate v, figure 78, of *longifolia* clearly shows the appressed marginal epidermes to the right and the twin bundles of the midrib to the left, the ovules being inserted at the margins.*

As we return to a consideration of the residue of the dome, it must be realized that the great growth taking place in the ovule-bearing organ, and the difficulty of finding the perfectly median section with respect of two axes of possible obliquity, make the demonstration of that residue more difficult in later stages.

The oldest stage of the residues of the dome yet illustrated (Plate ii, fig. 18 for *longifolia*, and Plate iv, fig. 37 for *suaveolens*) shows the ovule-bearing organ extending for 0·09 and 0·125 mm. respectively above the insertion of the adjacent stamens. Plate v, figure 60, *a–b*, is from the stage in *longifolia* where that distance is about 0·2 mm., just before formation of the ovule initials. Some of the cells of the residue have a copious deposition of the substance that stains deeply with safranin and haematoxylin. Growth in this region appears to have been by cell enlargement only. The surface of the residue is now vertical or even leans outward, so that it has the appearance of being merely part of the surface of the pedicel or stipe of the ovule-bearing organ. The large cells of the pith, many containing the deep staining deposition, are seen to extend past the residue of the dome, between it and the mid-rib of the ovule-bearing organ. The corresponding figures (Plate iv, figs. 40–41) for *suaveolens* are from a slightly older stage when the ovule-bearing organ extends about 0·25 mm. above the insertion of the adjacent stamens. By this stage the ovule primordia have been formed. The same features just described can be observed here, except that there is not such a marked deposition of deep staining substance and the residue of the dome is not so far displaced from its original position. The upper part of the dome is "clasped" by the folded ovule-bearing organ in this species, so that its upper surface is less easily discerned in the later stages. This difficulty is illustrated in Plate iv, figure 42, of the stage of primary megasporogenous cells.

Two further stages are illustrated, about the times of the megaspore mother cell and the functional megaspore, in *suaveolens*. Comparing the earlier of these two stages (Plate iv, figs. 43–46, consecutive sections) with Plate iv, figures 40–42, it will be seen that much of the growth at the base of the ovule-bearing organ and all in the residue of the dome is by cell enlargement. The cells of the pith, some of them with the deeply-staining deposition, extend into the organ between its midrib and the residue of the dome. The lower part of the surface of the residue of the dome is now vertical (about 6 or 7 cells in the L.S.), the upper part (about 4 or 3 cells) is still curved and is "clasped" by the arms of the ovule-bearing organ. The slight mutual intrusions of the epidermal cells in this region make it difficult to follow the surfaces clearly, foreshadowing the almost complete obliteration of them, which is nearly accomplished by the stage of the functional megaspore (Plate iv, figs. 47–50). In this last stage, the tissue of the residue of the dome can still just be identified, though, had it not been

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* Note that the twin bundles of the midrib are formed from a single primordium.
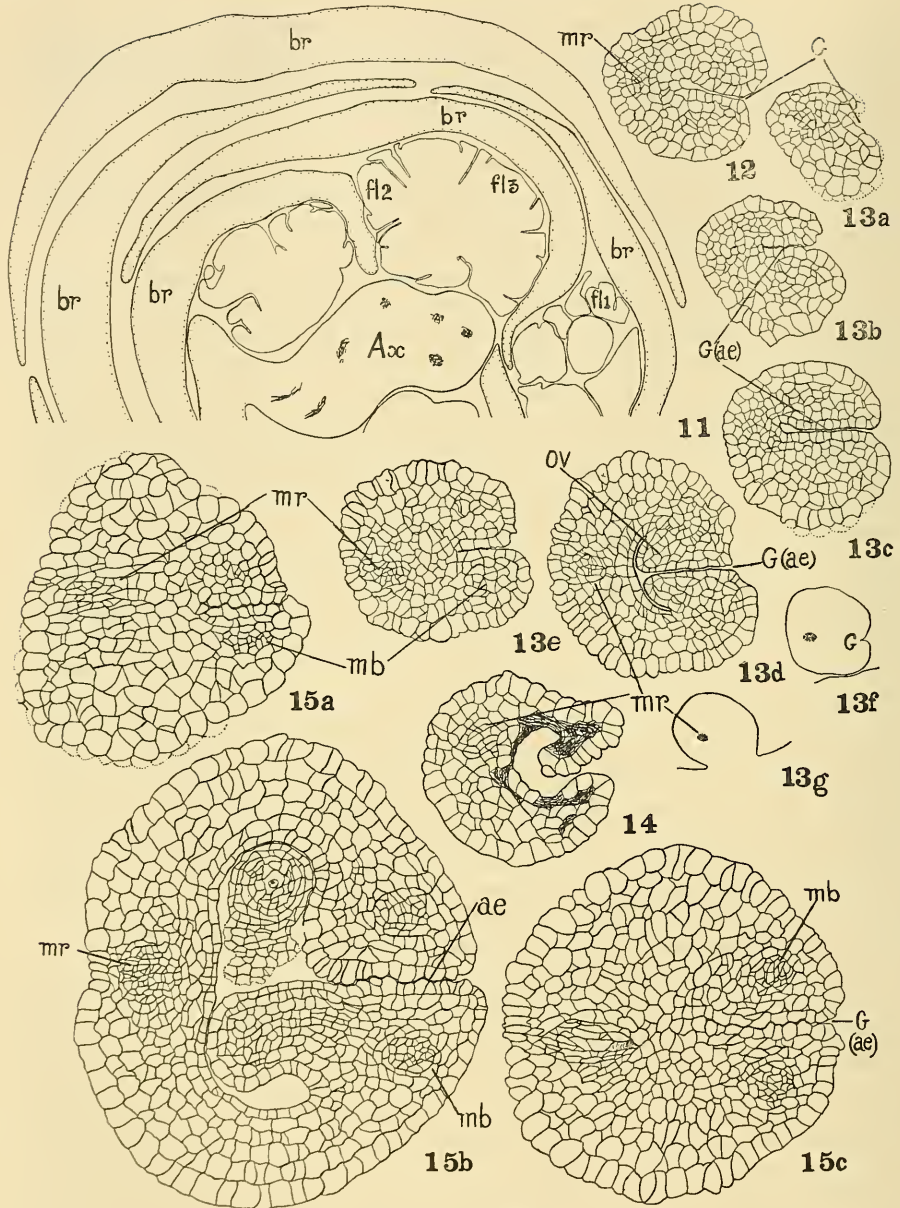
Text-figures 11-15c.—*Acacia suaveolens.*

11.—Transverse section of a little more than a longitudinal half of a raceme, showing the axis (*Ax*) giving off a pedicel of a flower-head to the left, sections of three flower-heads and several bracts. *fl1-fl3* are flowers of which sections are shown in Plate v, figs. 66-68. This figure shows the tight packing of the raceme with the bracts and the resultant distortion of some of the flowers. Magnification, × 55.

12.—Transverse section about half-way up a young ovule-bearing organ of 0·16 mm. length, before the formation of the ovule primordia. Magnification, × 160.

traced from the beginning, it could not have been discriminated from the tissues of the base of the ovule-bearing organ. The disposition of the pith and the deposition in its cells in this stage are but continuations of the conditions in the earlier stage just described.

The development of the vascular tissue has not been followed far, but it is evident that the pith extends between the residue of the dome and the single pro-cambial strand of the early stages of the ovule-bearing organ (Text-figs. 6–7*e*, 12–13*g*, Plate v, figs. 60*a–b*, Plate iv, figs. 40–41). During the development of the ovules, pro-cambial strands are differentiated beneath them in the margins of the ovule-bearing organ (Text-figs. 10*a–c*, 15*a–c*, Plate v, figs. 76, 78 and fig. 77).

Though I have not traced the residue of the dome in *longifolia* beyond the stage shown in Plate v, figures 60*a–b*, this description is not thereby made appreciably incomplete, because at that stage the residue of the dome was situated further below the folded arms of the ovule-bearing organ, the later development of which could not complicate the description as in the case of *suaveolens*.

INTERPRETATION OF THE EVIDENCE.

INTRODUCTORY.

The foregoing description of some of the aspects of floral ontogeny in *Acacia suaveolens* and *Acacia longifolia* is made in order to provide a basis for the morphological interpretation of the legume, and to contribute to the morphological interpretation of the carpel. As Schüepp (1930, p. 339) says: all forms are produced by growth, and therefore morphology must always become more a story of formation (Bildungsgeschichte). Having described in detail the appearances of the different stages of that story, we now have to make an interpretation of them, remembering that the floral apex is a living, re-acting organization. It is, however, necessary for the sake of clearness to make some temporary restriction in the angle of approach to the subject. The description has, therefore, been made in terms of the histogenesis of an apical meristem giving rise to lateral organs. In the literature available to me I can find no such account of a floral apex, and very little reference in the citations. The aim of this paper is to use the histogenesis as a basis for interpretation, and not to make a detailed study of histogenesis in the floral apex. It has therefore been necessary to employ one of the methods of description already in use for the vegetative apex. The description I have given has been based on accounts of the apical meristem that are generalized and describe activity, rather than on those that are precise demarcations of tissue-areas and describe appearances.

Louis (1935, p. 92, footnote) defines his terminology for the early stages in leaf formation thus: "initium foliaire" is the very beginning of divisions that form a protuberance, "primordium foliaire" is still strongly meristematic, "ébauche foliaire" is the protuberance in differentiation. In the terms "initial",

13*a-g*.—Representing a series of 40 transverse sections of an ovule-bearing organ with primordia of the ovules. Sections are 6*μ*, the numbers represented being 2, 4, 7, 21, 29, 30 and 34, beginning at the tip. Note the continuation of the groove to the tip of the organ, and the ovules arising at the edges of the incurved arms of the groove. Magnification, × 160 for *a-e*, and × 80 for *f-g*.

14.—Transverse section of a young sterile ovule-bearing organ that had not formed primordia of ovules. Magnification, × 160.

15*a-c*.—Transverse sections of an ovule-bearing organ at the stage of the mother cell, through the junction of style and loculus, the region of ovules and just below the region of ovules. Plate v, figure 77 is of a section through the base of the loculus of this organ. Magnification, × 160.

"primordium" and "young . . ." I have generally followed that system.   (There
are no sharp boundaries between the stages.)

The examinations made in this inquiry were directed primarily to tracing the
initiation of the parts of the flower, and especially the relation of the legume
to the apex.   There is not enough detailed evidence collected to permit of much
reference to the origin of the vascular tissue and the connection of the vascular
strands of the floral parts with the axis.

References in the literature to the meristem of the floral apex* seem to be
concerned mainly with physiology or the determination of time and conditions
of flower formation for economic purposes.   Klebs (1914) has shown experi-
mentally that flower formation is related rather to quantitative seasonal
differences in nutrition than to qualitative differences in the substances supplied
to the growing apex.   Schmidt (1924) records that in *Scrophularia* the
meristematic layers lie more thickly at the apex at the time of flower formation.
Priestly (1929, p. 63) suggests that the greater depth of meristem in flower buds
is due to a greater thickness of cell walls and consequent increased water supply
through them to the protoplasts; the thickness of the walls is possibly correlated
with the relatively greater proportion of carbohydrates in the supplies to the
apex at the time the flowers are being formed.†   More closely placed to our
present problem are the many papers on the formation of "fruit-buds" (e.g.,
Barnard and Read, 1932–3, references to literature), which appear to cover the
ground required, but not in sufficient detail of description or illustration to give
any information on the histological details of the floral apex.   Such workers
must have a great deal of material that would throw light on histogenetic
problems of the floral apical meristem and on the morphology of the carpel.

So little work, then, has been done on the histogenesis of the floral apical
meristem, that caution must be exercised in drawing conclusions in the absence
of detailed and systematic examinations.   This paper will have served a useful
purpose if, in attempting to describe the floral in terms of the vegetative apical
meristem, it calls attention to the great field of work here to be found in
connection with morphological inquiry.

THE VEGETATIVE APEX AS A BACKGROUND FOR THE INTERPRETATION.
The Apical Meristem.‡
Structure.

We owe our knowledge of the structure of the cells of the apical meristem
of the angiospermous shoot largely to Sachs (1882), Schmidt, Schüepp, and
Priestly.   Differing slightly in details, there is a general agreement among them
that the cells occur in zones that are more or less sharply defined, and of various
numbers of cell-layers.   The outer zone is composed of regular, straight-sided,
rectangular cells with relatively very large nuclei and dense, unvacuolated
cytoplasm, which assume their shape on account of external pressure, having no
internal (osmotic) pressure due to vacuoles (Priestly, 1928, pp. 4–6, and 1929,
p. 55).   There follows a zone of cells which, though still dividing as rapidly as

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* A paper by Grégoire (1931) is not included here, as it is a subject of criticism
on account of the morphological conclusion.   It is dealt with below (p. 79).

† In some species of *Acacia* (e.g., *Baileyana*) flower formation and vegetative growth
appear to go on at the same time.

‡ I regret that Schüepp's monograph on the Meristem (1926) is not available to
me in Sydney.   I therefore ask to be pardoned if any of my deductions that follow
appear to repeat existing discussions unnecessarily.

those in the outer zone, are in process of becoming vacuolated. Within and below is a zone of cells which, having attained vacuolation, are expanding by the intake of water into the vacuoles. The outer zone is described as "meristematic" (Priestly, 1929, p. 54), "typical" and "embryonic meristem" (Schüepp, 1917, p. 73, and 1926), and "tunica" (Schmidt, 1924). The almost complete predominance of divisions with anticlinal wall-formation, makes its one to about four layers of cells genetically distinct. The next zone has been described as "vacuolating dividing" (Priestly, 1929, p. 54) and "half-meristem" (Schüepp, 1917, p. 73, and 1926). The direction of the nuclear divisions in it is at random. The third zone is described as "vacuolating expanding" (Priestly, 1929, p. 54) and "lengthening tissue" (Schüepp, 1917, p. 73, and 1926). The last two zones comprise the "corpus" of Schmidt (1924).*

We must not expect these zones to be rigidly marked; for example, Foster (1935, p. 90) refers to occasional periclinal division-walls in the "tunica" of *Carya Buckleyi*. Priestly (1928, pp. 11, 12) points out that the definiteness of organization of the zones of the meristem depends on the rate of growth, degree of internal pressure (due to vacuolation and expansion of innermost zone) and breadth of the apex.

The description given of the structure of the meristematic tissues of the floral apex of *Acacia suaveolens* and *Acacia longifolia* are in general agreement with the terms outlined above. Before discussing the results of the activity of the vegetative apex, certain internal and external conditions affecting its operation will be pointed out.

According to Errera's law, new cell walls are formed in such a direction that they are of minimum area (Errera, 1886).† The truth of this was demonstrated by Giesenhagen (1909). It seems quite reasonable to consider with Zimmermann (1928, p. 313) that the function of the "corpus" (Schmidt, 1924), comprising the zones that are vacuolating and that are expanding (Sachs, Priestly and Schüepp), is the extension of the vegetative point, for the random direction of division walls (vacuolating zone) and the expansion of the cells by intake of water (expanding zone) will produce increase in volume (expressed mainly as increase in length). On the other hand, as many have pointed out, the outer zone, by its divisions with anticlinal wall formation, produces only increase in surface. Priestly (1928, pp. 10, 11) has suggested that the pressure set up by the vacuolation of the internal zones compresses the outer zone of fully meristematic, unvacuolate cells against the cuticle, so that, not only are they of a rectangular shape, but their long axis is parallel to the surface. The result is that the minimum area across which new walls can be formed is perpendicular to the surface of the growing point, thus instituting the difference between the zones of anticlinal and random direction of wall-formation. The growing point thus appears within itself to be differentiated as the expression of a system of pressures and tensions. The increase in surface of the outer zone is a direct result of the pressure due to increase in volume of the inner zones. There is a paradox here which will be explained further on.

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* In addition, Schüepp (1917, pp. 60-68) describes in *Helianthus annus* an apical group of initial cells that give rise to the two zones of meristematic cells. In the figures given by Priestly (1928, 1929), Priestly and Swingle (1929), Zimmermann (1928) and Louis (1935) I can recognize no such group.

† The term used in this reference is "average constant curve" (courbure moyenne constante).

Usually the apical region of the shoot, particularly when the apical cone is short, is closely surrounded by the young leaves, which have every appearance of being pressed against it. The lower part of the apical cone is in contact with the surface of the youngest leaves. Increase in volume of the cone would cause flattening of the outer layers of cells of that part of the apex. The consequent operation of Errera's law to produce anticlinal wall-formation would tend to emphasize the growth in surface along the faces of the existing leaves, that is, growth would be parallel with the surface of pressure. This may explain the origin of new leaves *between* the existing ones, where the conditions can favour divisions with periclinal wall-formation, and folding of the surface into the free space to accommodate the increase opposite the existing leaves. It seems, there-fore, very reasonable for Schüepp (1917) to emphasize strongly that (following Sachs, 1894—with some modifications) the direction and growth of each meristem cell is consequent upon the form of the whole vegetative apex and upon its position in the apex (p. 61); and to conclude that the external differentiation of the vegetative apex is primary, and the inner differentiation consequent thereon and secondary. Though a reversal of existing ideas, this leads to a theory which may explain the progress of the vegetative point from an undifferentiated to a differentiated condition (p. 75).

We have now seen that it is possible to look for quite simple explanations of the external and internal differentiation of the vegetative apex. These simple explanations would not be all-inclusive;* they also assume the process of apical growth to be in progress; and there still remains the problem of how the process is started. However, the above ideas will serve as a useful check on interpreta-tions that may be too rigid or artificial.

Activity.

It has already been pointed out that the manner of growth of the outer, "fully meristematic" (unvacuolated), cell-layers produces increase in surface of the apex, and that the manner of growth of the two inner zones produces increase in volume. It has been shown by Schüepp that the rate of division in the different meristematic layers is the same, regardless of the depth from the surface. He has calculated that such a condition will produce an increase in surface greater than that necessary for the increase in volume. The result is that the surface of the apical cone is thrown into folds which become the initials of the leaves (Schüepp, 1914, pp. 335–338; 1917, pp. 62, 64–68; 1930, p. 340). Priestly (1929, p. 62) supports this and points out that the layer(s) immediately under the fold are generally subject to divisions with periclinal wall-formation whereby they contribute to the primordium of the leaf. (See also Schüepp, 1930, p. 340). If the fold in the outer layer draws out the cells of the next layer(s) so that their long axis is perpendicular to the original surface of the apical cone, it is under-standable why the division walls should be periclinal. One of the chief results of the process is that the leaves are formed from the two to four outer layers of the apex. Though he does not express it in terms of "folding", Zimmermann (1928, pp. 303, etc.) describes the origin of the leaves in *Hypericum uralum* from the four outer layers ("tunica" of Schmidt, 1924, and the "fully meristematic" zone of Priestly, 1929), by divisions with anticlinal wall-formation in the first and second layers and enlargement and divisions with periclinal wall-formation in the third and fourth layers.

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* I have not taken the physico-chemical conditions of the apex into consideration, as I have derived from my investigation no information thereon.

Two difficulties now arise. First, there is the paradox referred to above, namely: if the surface is increasing in excess of the volume, how can the outer layers be compressed between the cuticle and the expanding inner zone? The second difficulty is: if the meristematic layers are all growing equally fast, and therefore produce folds in the surface, why are these folds localized and not as rings round the apical cone?

It is a matter of observed fact that growth is not uniform over the whole circumference of an apex.* Priestly and Scott (1933, p. 242), speaking of the emergence of leaf primordia, have said: "In phyllotaxis the actual locus of a new emergence becomes very important. Unfortunately all that can be said is that every meristematic apex is apparently asymmetric and grows more rapidly at one point than at any other. This point becomes the centre of a new fold." Priestly (1929) and Griffiths and Malins (1930) have described a unit of shoot growth which does not occupy the whole of the circumference of the shoot. If this is associated with any form of spiral phyllotaxis, it requires a revolving segment of increased activity in the apical meristem, producing isolated folds by an intermittent movement. Schüepp (1914) has measured the period of this movement and found that it is rhythmic, with a time interval which is constant for any one organ of a species. This interval is the "plastochrone" (Askenasy, 1880, p. 76), which may be associated with movement of the segment in one or more spirals. Schüepp (1921) has worked out the geometrical relation-ships of different types of known leaf arrangements, assuming such a periodical raising of equal parts from the embryonal mass of the vegetative apex.

Thus the second difficulty is explained by the fact that, though the rate of meristematic activity is uniform in the meristem perpendicularly to the surface, it is not uniform parallel to the surface but is more intense in a restricted segment, subject to periodic fluctuation and displacement. The explanation of the first difficulty begins at the same point. For over most of the surface meristematic activity is not occurring at greatest intensity (if at all†). It seems reasonable to assume that the expansion due to vacuolation will not be subject to localization like the meristematic activity and will set up a more or less constant pressure, preparing the outer layers in the more slowly growing segment for the anticlinal wall-formation to follow.

There has been outlined above a mechanism of growth which is simple, and operates through internal and external conditions that do not require rigid and artificial definitions, but allow of a reasonable merging of processes and indefinite-ness of structural zones. (Zimmermann, 1928, p. 342, concludes that the relation-ship of the layers of the apex to the leaf varies from case to case.) It is on such a basis that I have built the description in the earlier part of the paper, and upon which an interpretation thereof will be made later.‡

* Cf. the nutation and circumnutation movements of apices.

† Absence of meristematic activity from a large segment of the apex would cause marked distortion which is not observed in every case. Activity at the very apex may be uniform (cf. Schüepp's group of initial cells, 1917, pp. 64-66) and the operation of the varying intensity of activity be confined to a region a little below the apex.

‡ Certain work on the processes of the vegetative apex should be mentioned here, though it is disregarded in the background for the interpretation made in this paper.

Schmidt (1924) has used the idea of an alternation of minimum and maximum area (minimalfläche and maximalfläche) during a plastochrone, so that the growing point increases during the interval from a minimum area to a maximum area, at the edge of which the initials of the new leaves arise, reducing the growing point to a minimum area again. Louis (1935) and Grégoire (1935a) have made strong use of this idea.

The Lateral Organs.

This inquiry does not follow the development of the lateral organs very far, and has little to disclose about their vascular connection to the stem.   There seems to be general agreement that, as we pass down the young axis, we find that vacuolation takes place not only at the centre but at the periphery, leaving a ring of meristematic tissue ("pro-desmogène" of Grégoire, 1935*a* and *b*, and Louis, 1935) which becomes the locus of the procambium; though not necessarily all of it becomes procambium.   It is also to be noted that this process of vacuolation leaves a zone of meristematic tissue extending from the axial ring into the meristematic tissue of the primordium of the leaf.   (See Priestly, 1928, pp. 12–14, and 1929, p. 74, for the institution of the vascular connection.)

Louis' description (1935) of the tissues of the young leaf of several species, including *Syringa vulgaris* and *Arabis alpina*, is important for our purpose.   The primordium is first evenly meristematic throughout its volume.   Then, a little distance below the tip of the primordium, vacuolation begins on the ab-axial and ad-axial sides, leaving an arc of meristematic tissue joining the margins of the primordium and extended upwards to occupy the whole of the cross-section at the tip.   Further vacuolation across this arc leaves meristematic tissue at the margins and in the centre of the young leaf.   From the marginal meristems, the lamina is developed.   The central meristem is the locus of formation of the pro-cambium.

Residual Apex.

As the vegetative shoot is theoretically of unlimited growth, the question of a residual apex does not arise in the investigations of its manner of growth. There is, therefore, no body of information against which to set the discussion of this question which must arise in considering the growth of the flower which is

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I have disregarded it because it seems to be really a description of the appearances only, whereas the ideas of Schüepp and Priestly, set out above, take us into the realm of explanation.

Grégoire (1935*a* and *b*) regards the leaf primordia as arising on "leaf foundations" (soubassements foliaires) developed on the vegetative cone as it increases from minimum to maximum area during a plastochrone; and that on account of this "foundation" the leaf grows vertically.   This is described with illustrations by Louis (1935, pp. 99-123) for *Syringa vulgaris* and *Arabis alpina,* together with details of the shape of the cone at successively lower levels, including the "foundations".   Using these terms, Louis finds it necessary to formulate two types of leaf initiation in the Dicotyledons: (1) Alternation of minimum and maximum area with the establishment of the leaf foundation, the general type; (2) The development of a lateral protuberance, in a few cases such as *Hippuris vulgaris* (pp. 126-130).   Zimmermann has described in *Hypericum uralum* the histogenesis of the same phenomenon that Louis describes as "soubassement foliaire", without recourse to the terms used by Louis and Grégoire (Zimmermann, 1928, p. 303, etc.).   It seems to me that Louis and Grégoire, in their interpretations, have failed to recognize that the pressure from within the apex and the restrictions imposed from without by the existing leaves will in a great degree determine the shape of the vegetative cone and the shape and direction of growth of the primordia.   The recognition of these factors will obviate the necessity to formulate the two types of leaf initiation in the Dicotyledons, and will prevent what seems to me too rigid and artificial a description of the phenomena.

Support for the recognition of the influence of pressure by existing organs comes from Doak (1935), who refers to the bud scales of *Pinus* having a *"binding effect* upon the tissues within" (p. 24); and speaks of certain phases of evolution in *Pinus* where "Just as pressures within the compound bud *limited, shaped,* and *displaced* the sheath scales of the dwarf shoot, so the formation of the compound strobilus *limited, shaped* and *displaced* the sporophylls on the simple strobilus" (p. 43).

theoretically of limited growth. The following considerations have a bearing on the question.

If it is correct to consider with Zimmermann (1928, p. 313) that the vacuolating dividing cells and the expanding cells ("corpus" of Schmidt, 1924), have the function of extending the vegetative point, and with Priestly (1929, p. 69) that the vacuolating dividing cells characterize "that region of cell growth and activity which lays down the node and internode of the 'articulate' shoot organisation"; then, in a shoot of limited growth, it is in that region we must look for the beginning of an explanation of the limitations of growth.

Two other observations of vegetative apices are significant for the question of a residual apex. Schüepp (1914, pp. 332–3) studied growth curves in *Lathyrus latifolius* L., and suggested that the initial, rapid growth of the laterals, followed by slow growth, is due partly to diversion of material to the new ones, leaving a deficiency for those already formed. Priestly and Scott (1933, p. 242) consider that the early formation of pro-cambial cells is probably responsible for the fact that the leaf primordium grows more rapidly than the meristematic apex; and conclude (p. 266) that primordia, once formed, are competing centres of activity. Schüepp (1917, pp. 45 and 76) correlates the proportion of the vegetative cone involved in the formation of a lateral with the number of shoot parts growing at any one time (i.e., with the length of the plastochrone). In *Elodea*, where one-tenth of the apex is used up, many parts are growing at one time; but in *Mesembryanthemum pseudotruncatellum*, where nine-tenths of the apex is involved, only one or two parts are growing at the one time. In the latter case there is a long rest period. It is conceivable that if the growth rate of the apex were otherwise slowed down, the superposition of the rest period might cause such a delay that the extent of growth of the last-formed lateral might mechanically and/or physiologically prohibit further growth of the apex, before the completion of the rest period.

If meristematic activity occurs periodically in sectors disposed in a spiral manner on the growing cone, then, under the conditions just indicated, it seems reasonable to conclude that in a shoot of limited growth there must be a residual apex. No organ could be strictly terminal.

<div align="center">THE INTERPRETATION.</div>

We come now to review the description given of the floral apex in *Acacia suaveolens* and *Acacia longifolia*, making an interpretation against the background of the foregoing discussion of vegetative apices. In this interpretation the term "carpel" will not yet be used. In examining the photomicrographs, allowance must be made for slight shrinkage in the fully meristematic cells.

<div align="center">*The Apical Meristem.*</div>

The floral apex in both these species exhibits three zones of cellular condition: the fully meristematic zone with dense, unvacuolate cytoplasm, relatively large nuclei, rectangular cells and predominance of anticlinal wall-formation; the half-meristematic zone with the beginning of vacuolation, relatively large nuclei and random direction of division; and the vacuolating expanding zone without division but with enlargement of cells by intake of water into the vacuoles and with curved cell walls. That there is not complete regularity of direction of division in the outer zone is probably due to the apex being broad (Priestly, 1928, p. 12), with consequently less pressure to flatten the outer layers. Probably, it is also partly due to a lessening of the pressure on account of the diminishing expansion of

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the inner zones concurrent with the limitation of growth. This diminishing expansion of the inner zones is explained by the fact that the vacuolating dividing zone appears frequently to consist of one layer only, and rarely of more than two. If these expanding zones are normally the cause of growth in length, we are witnessing the limitation of that growth.

The Sepals, Petals and Stamens.

There is the regular formation of the initials of the sepals and petals by folding of the outer layer of cells and the projection into the fold of the next layer or two, mostly by divisions with periclinal walls.

The formation of the shoulder is an interesting variation from the growth of a vegetative apex. I doubt whether there is any special significance in it. A possible explanation is that the external restrictions of the growing petals cause them to compress tangentially the adjacent cells of the outer zone of the apex so that the operation of Errera's law results in divisions with periclinal wall-formation.

Although the formation of the stamens appears to follow the normal process of folding of the outer layer with periclinal wall-formation below it, there is to be sought a reason for the sudden change in the size of the folds compared with the initials of the sepals and petals. Is it due to a diminished size of the segment of meristematic activity? That here we have many parts growing together can be correlated with the fact that in the formation of any one of them only a very small fraction of the apical cone is used up. There is no evidence against their formation in spiral sequence. They are not formed simultaneously.

The Relation of the Legume to the Apex.

The formation of the shoulder leaves the central part of the apex as a small dome composed only of fully meristematic cells. By the time the stamen primordia are all formed, this dome, which is all that is left of the meristematic apex, has increased in size slightly. This increase, due almost entirely to cell enlargement, is laterally restricted by the growing stamens and the other parts of the flower so that the small apex is forced to extend vertically by elongation of its cells. As the vacuolating dividing zone does not extend into the apex, there is no means of producing a normal lengthening of it. At this stage the vacuolating dividing zone has almost been changed into the expanding zone. Apical growth has nearly ceased.

By the asymmetric incidence of meristematic activity, a lateral fold is formed in the outer layer of the apex; the lower layers protrude into the fold by divisions with periclinal wall-formation; and thus the initial of the legume is formed in the same manner as those of the other parts of the flower *and of vegetative leaves*. The small radius of the apex at the time causes the initial to have a strongly curved insertion, so that the primordium is curved from the beginning. The growth of the primordium is not just a vertical extension from its insertion on the apex. The meristematic tissue at the tip increases the length, and the meristematic tissues on the margins extend the breadth of the lamina of the legume. The legume is thus initiated and the plan of its structure differentiated in the same manner as for vegetative leaves. The spatial restriction to which it is subjected forces it into a vertical position. Excess growth in the abaxial part causes the marked curving which produces the close contact of the margins, whose appressed epidermes at later stages undergo a slight mutual intrusion which nearly makes them indistinguishable. The ovules are produced

at the margins of the lamina of this leaf-like organ, the legume, which has been so folded that they develop into an enclosed space. Above the region of formation of the ovules the growth of the margins and the excess growth on the abaxial side diminish acropetally, so that the central cavity is continuous upwards with a closed groove which becomes merged into the surface of one side of the cylindrical style. The groove reappears at the tip of the style as the stigmatic surface, which is slightly depressed and laterally displaced.

After the formation of the initial of the legume, the residue of the apex (dome) passes from the fully meristematic condition to a condition of complete vacuolation without further meristematic activity (even in the early stages of the process). We have thus witnessed the suppression of the apex,* which is displaced laterally and overtopped by the developing legume. Slight mutual intrusion of the epidermes of the residue of the apex and of the lamina of the legume (where the two are in contact) makes it almost impossible to distinguish them in the later stages. At a period later than shown in this paper the residue of the apex would assume the appearance of being but a small part of the short stalk of the legume.

The relation between the early development of the legume and the suppressed apex has been demonstrated by a series of models made in "plasticene" (modelling material). These models were made differently from those described earlier. They were moulded by hand according to measurements of certain of the illustrations of *Acacia suaveolens* in this paper (see explanation of the Figures for identification). They are of the same magnification as those illustrations (approximately). White plasticene was used to represent the apex just before the formation of the initial of the legume, and the residue of that apex thereafter. Grey plasticene was used to represent the legume at all stages of development. These models were cut longitudinally so that the cut surface would present the same aspect as the illustrations upon which they were based. The complete models are shown in Plate v, figures 61–65. The cut models are shown in Plate v, figures 71–75, together with the originals from which their measurements were taken. The gradual displacement of the suppressed apex, and the clasping of its top by the base of the lamina of the legume, is clearly shown.

On the evidence brought forward in this paper, I can see no other conclusion than that the legume in the two species examined is a lateral laminar organ developed on an apex which is immediately suppressed; that the initiation and differentiation of the legume is not significantly different from those of a vegetative leaf; and that the ovules are formed on the margins of the lamina of the legume.

<div align="center">

DISCUSSION.

INTRODUCTORY.

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This histogenetic study of the floral apex and initiation of the floral appendages of *Acacia suaveolens* and *Acacia longifolia* has been designed to test recent criticisms and variations of the classical idea of the carpel as a modified leaf. The evidence presented herein is the cellular details of the meristematic activity of the floral apex that gives rise to the initials of the floral organs. In the case of the legume, the study is continued as far as the formation of the ovule primordia. This evidence shows clearly that (1) the legume takes its origin by the meristematic activity of cells occupying a lateral position on the floral

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* See above ("Residual Apex", p. 72) for possible causes.

apex; (2) the residue of the apex loses its meristematic activity, the apex thereby becoming suppressed; (3) the legume is a single, laminar structure which by incurving and adpression of its margins encloses a central cavity; (4) the ovules arise on the incurved margins of this laminar structure.

The work of Priestly and Swingle (1929) on regeneration has emphasized the fact that cells can resume the meristematic state long after they have lost it, if the appropriate conditions are set up. This obviously happens after fertilization, when the legume renews its growth. There is therefore no reason against renewed meristematic activity producing vascular tissue in the uppermost parts of the floral axis where there were no procambia at the time of formation of the legume primordium. It would then be easily possible for the pod to appear to receive the whole of the residual vascular cylinder after the exsertion of the androecium. The minuteness of the residual apex alone, before or after the renewed meristematic activity, might also cause this appearance. At the time the first procambia are formed in the primordium of the legume, the vertical distance is very small within which the level of their insertion is to be determined—in the cases of *Acacia suaveolens* and *Acacia longifolia* it is only about 50μ. Differences in level within such a distance may easily be obliterated or even reversed by the growth that takes place up to the stage of fertilization, and still more so after fertilization. It is reasonable, therefore, to regard a study of the vascular anatomy after the very earliest stages as being not competent to determine whether or not the legume is terminal. This is especially so if transverse sections only are used. (The same considerations would apply to any gynoecial structure under morphological interpretation.) Moreover, a multitude of the types examined can add no weight to any conclusions, if the manner of examination is not competent to reveal significant evidence.

In this paper I have studied ontogeny and meristematic activity. That is to say, a close series of stages of the coming into being of the parts concerned has been examined and illustrated with cellular details of the meristematic tissues involved. This study has led to interpretations different from some that are claimed to have as their basis an examination of ontogeny and meristematic activity, or that follow expositions of the necessity for such examinations (Grégoire, 1931, pp. 1288–9; Thomas, 1934, p. 177; Thompson, 1931, p. 75, and 1934, p. 7). The studies of these workers appear to me to lack the necessary closeness and earliness of the series of stages described, the presentation of cellular details of the tissues and the illustration of longitudinal sections. There is serious danger of calling "ontogeny" that which is not ontogeny because it includes so few truly early developmental stages and is not of sufficient detail.

For the reasons outlined above I have taken little notice of vasculation after the primordial stages, in this inquiry, and will not make much reference thereto in discussing the literature. The questions of the vascular anatomy of the legume will be found discussed with references to the relevant literature in papers by Parkin (1929), Eames (1931), Arber (1933), Bancroft (1935), Joshi (1935), etc., in addition to the four propounders of the theories I am discussing.

CRITICISM OF RECENT THEORIES.

We now come to consideration of the theories of the four workers mentioned at the beginning of this paper who oppose or modify the classical theory of the carpel. It is to be understood that I can only speak in so far as they refer to the legume—particularly the *Acacia* legume—or make reference to the carpel in

general. There will not be a detailed comparison of the evidence produced in this paper with the evidence and conclusions given by these writers. But I will ask the reader to bear in mind the content and nature of the evidence presented herein and the remarks made above on the competence or incompetence of different types of evidence. The common elements of the different theories will be discussed together.

If the evidence, the interpretation, and the criticisms of types of evidence that have been given above are valid, then the following propositions are not true: (1) The legume is a terminal structure; (2) the legume is not a single folded structure; (3) the legume is not a foliar structure.

(1) *The legume is a terminal structure.*—This statement is made by Saunders (1929). She bases it on the claim (p. 225) that the "whole residual vascular cylinder in the Leguminosae is continued directly into the gynoecium". The evidence presented in support of this claim consists of transverse sections of well advanced legumes shown in outline, with no significant illustrations of cell detail. There are no longitudinal sections, no close series of early developmental stages nor an exposition of terminality being a necessary consequence of the whole residual vascular cylinder* entering the gynoecium. For *Acacia suaveolens* she produces no evidence on this question, because Figures 1–3 do not include the level of exsertion of the legume from the floral axis.

In making this statement, Thompson† (1929, pp. 16–17, etc., and 1931, pp. 11, etc., and 75—conclusion) appears to have regarded the "dome", that is, the remainder of the apex after the formation of the stamens, as the initiation of the legume. The evidence he presents (neglecting sectional views of adult flowers) consists almost entirely of outline drawings of serial transverse sections at various stages of development. The one longitudinal section illustrated is of *Acacia spadicigera*, and demonstrates clearly the necessity for the study of tissues (1931, fig. 63). The outline of the "gynoecium" in this figure is almost identical with the outline of the legume plus the residue of the apex shown in my Plate ii, figures 13–15, and Text-figure 4 for *Acacia longifolia* and Plate iii, figures 31, 32, 34a and 35 for *Acacia suaveolens*.

Grégoire (1931, pp. 1289 and 1294) makes the statement with regard to the carpel in general. His figures are very few and show no developmental series or details of tissues (see Postscript, p. 88).

Arber has discussed cases of leaves that are described as terminal (1930, pp. 301–2). One of these is that of *Gigantochloa* (1928, p. 184); but in the evidence presented there is the same lack of close developmental series and cellular detail of tissues. Attention is re-directed to the tentative argument made above that an organ cannot be terminal.‡

If the legume is not terminal, we expect to find some cases where the apex has not been suppressed. Such a case was found in *Acacia Baileyana*, where an apex had produced a young flower after the formation of the legume. The young

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* This question of the "whole residual vascular cylinder" is bound up with the conception of the unit of shoot growth. Cf. Griffiths and Malins (1930) and Priestly and Scott (1933).

† In a later paper (1934) Thompson propounds a theory which is incompatible with this, but he does not definitely withdraw his frequent and unequivocal statement of terminality of the legume made in the papers referred to here.

‡ See "Residual Apex" (p. 72). Also compare the idea of the unit of shoot growth (Griffiths and Malins, 1930, and Priestly and Scott, 1933).

flower had the appearance of growing out of the base of the legume (Newman, 1933, p. 154).

If the ontogenetic and histogenetic evidence presented in this paper is representative of the evidence that could be produced from other Leguminosae by similar methods of study, then the legume is a lateral organ. The legumes of *Acacia suaveolens* and *Acacia longifolia* are certainly lateral organs.

(2) *The legume is not a single folded structure.*—This proposition is part of Saunders' application of the Theory of Carpel Polymorphism to the Leguminosae (1925, p. 142, and 1929). Her statement that the legume consists of two carpels, one fertile and the other sterile, is incompatible with the ontogenetic and histogenetic evidence given herein* for *Acacia suaveolens* (illustrated by her, 1929, Figs. 1–3) and *Acacia longifolia* (referred to by her, 1929, p. 227). She illustrates with outline drawings of transverse sections (1929), except in two figures with cell detail, one of which (Fig. 79) shows the legume a single folded structure (the other does not bear on the point).

Grégoire (1924) regards the legume (of Papilionaceae) as not folded because he interprets its primordium as annular. In the cases described here the primordium is certainly not annular. The figure given by Grégoire is a transverse section of a legume long after the primordial stage. His objections to the single structure based on dehiscence have been met by the description of the pod of *Acacia Baileyana* (Newman, 1934, p. 238).

I can only conclude from the evidence presented herein that, if it is representative of what could be found by similar methods in other Leguminosae, then the legume is a single folded structure.† The legumes of *Acacia suaveolens* and *Acacia longifolia* are certainly single folded structures (similarly for *Acacia Baileyana*, Newman, 1933, pp. 153–6, and 1934, p. 238).

(3) *The Legume is not a foliar structure.*—In discussing the two preceding propositions we were dealing with descriptions of facts. The differences between the descriptions were due to differences in the methods of examination and presentation. This proposition introduces morphological interpretation, which is naturally influenced by our description of the facts, and consequently by the methods of examination and presentation.

Thomas (1931, pp. 660–2, and 1934, pp. 186-8 and figs. 12, 13A–C) has described the hypothetical evolution of the Angiospermous carpel from a cupular structure, beginning with a cupule like that of *Gristhorpia* (Caytoniales). He derives the follicle from such a form by fusion of two ovaries in such a way that the cupules became concrescent and, curving over, enclosed the ovules which were axial organs. In this process the last traces of the stem might be included on the side of the structure away from the ovules. From this hypothetical type he derives the legume. His comparative evidence (from present-day forms) in support of this hypothesis does not contain close ontogenetic series or illustration of cellular detail of tissues at the very earliest stages of development. The ontogeny of the legume presented in the present paper plainly shows the ovules to arise on the margins of a single folding laminar structure, a process incom-

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* Similarly for *Acacia Baileyana* (Newman, 1933, pp. 153–6, and 1934, p. 238).

† Thompson (1929 and 1931) has supported this view, though in a later paper (1934, p. 8) he seems to suggest a multiple structure, viz.: "Other forms of accepted carpel, such as the legume, likewise arise, singly or in series, by union of emergences from the sporogenous tissue of the axis." I cannot find where he has withdrawn the earlier view.

patible with a derivation such as suggested.† There is also incompatibility between the hypothesis and the ontogeny with regard to the stigma (cf. Thomas, 1934, fig. 13A–C).

Grégoire (1931, pp. 1288–9) says he will study: (1) the behaviour of the central part of the floral axis during formation of the carpel primordia, (2) the meristematic activity itself which originates the carpellary protuberances (ébauches), (3) the structure and activity of the floral meristem that produces carpel primordia compared with a vegetative cone concerned with the forming of leaves. He claims to find that (1) the centre of the floral apex forms or could form a carpel, (2) there are two distinct types of primordia, and (3) there are two distinct types of apical meristem. He concludes that the carpel is an organ *sui generis* and not a modified leaf (p. 1300). He does not show developmental series or cellular detail in illustration of his contentions. In the earlier part of this paper it has been shown in *Acacia suaveolens* and *longifolia* that (1) the legume is lateral to a suppressed apex, (2) the primordium of the legume arises similarly to those of vegetative leaves, (3) the structure and activity of the meristem of the floral apex is of a type known for vegetative apices (allowing for the limitation of growth).

The description of the legume as terminal and its interpretation as a phyllo-clade is made by Thompson (1929 and 1931). In a later publication (1934) he introduces a startling theory in which the accepted parts of the flower are discarded and replaced by emergences from a sporogenous axis (pp. 6–7). In reference to the legume he says (p. 8): "Other forms of accepted carpel, such as the legume, likewise arise, singly or in series, by union of emergences from the sporogenous tissue of the axis. . . . Whatever be their final state or form, they are here considered sporogenous phylloclades, in view of their origin from the sporogenous tissue of the axis. As they are enlarged, they carry with them portions of the original sporogenous tissue which may, locally, be sterilized. The sporogenous tissue carried by the phylloclades may be increased as growth proceeds. When ovules emerge from this sporogenous tissue, ovuliferous phylloclades are in being and not carpels, as commonly received." The evidence presented in the paper, which primarily deals with Scitamineae and Ranunculaceae, is largely diagrammatic and does not contain close developmental series, longitudinal sections or cellular details (except for one figure of an advanced stage). The detailed description of the developmental series with cellular detail of longitudinal sections given above for *Acacia suaveolens* and *Acacia longifolia* cannot be reconciled with that quotation.

It thus appears that the above theories, which deny foliar nature to the legume, are not compatible with the evidence of the ontogeny in *Acacia suaveolens* and *Acacia longifolia*. The evidence produced here is more detailed and of a more necessary type compared with the evidence shown in support of the theories referred to. It is compatible with the legumes of these two species (and by suggestion of all Leguminosae) being foliar structures.*

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† Joshi (1935) adversely criticizes Thomas's theory from the standpoint of anatomy. There is a reply added by Thomas.

* Judging from the description and figures given by Salisbury (1931, pp. 558-9, figs. 14-15 and Plate xviii, figs. 2-4) of the achene of *Ranunculus parviflorus* L., a close series of stages of development would show clearly the foliar structure with the ovule on the margin, though extreme reduction has caused the apparent axillary origin of the ovule.

POSITIVE IMPLICATIONS OF THE EVIDENCE.

We come now to attempt to assess the implications for morphological theory of the evidence and its interpretation that have been set forth in the foregoing pages. The enquiry began in order to investigate the claim that the legume of two species of *Acacia* is terminal and composed of two carpels, one fertile and the other sterile. In addition to determining those points in the negative, it has expanded into a description of the histogenesis of the floral apex in terms similar to those used by some writers in describing the meristematic activity whereby a vegetative apex gives rise to the emergences known as leaves. There are, therefore, two subjects for consideration. The first is the contribution to be made to the morphological understanding of the legume. The second is the contribution to be made to the morphological understanding of the flower.

It is clearly recognized that this discussion is of limited application, because only two species are examined, and the course of development is not traced far beyond the initiation of the primordia, except in the case of the legume. But there has been examined and illustrated, with cellular detail of close developmental series, the ontogeny of the floral apex, that is, the process whereby the undifferentiated (surface of the) floral apical meristem gives rise to the floral organs. It is claimed that such a study is the most essential requirement for morphological interpretation. Unfortunately, it seems to be very scarce in the literature of floral morphology.

The Legume.

It has been demonstrated that the legume is a single infolding laminar structure that arises laterally to the apex of the floral axis in a manner fundamentally similar to that of leaves on the vegetative apex, and that it bears ovules on the margins of the lamina. These facts are in harmony with the interpretation that it is a single carpellary structure of foliar nature. The final proof of the foliar nature would require more evidence than is provided in this investigation.

Foster (1935) finds a histogenetic difference between the foliage leaf and the cataphyll of *Carya Buckleyi* var. *arkansana* at a very early stage (0·09–0·1 mm. high) of the primordia, though they both arose from the same layers of the apical meristem. The difference lay in the distribution of the meristems within the primordia (pp. 101, 114, 124, 126). He refers (p. 88) to the conclusion of Schüepp (1929), that "differences in the distribution of types of tissue, and in the intensity and duration of their growth must form the basis for the difference between foliage leaves and bud scales". A comparison is therefore indicated of the distribution of the meristems in the legume with that in foliage leaves (of the same species especially). This aspect of the subject was only slightly examined by me, but the indication was that the distribution of meristems in the primordia of the legumes of *Acacia suaveolens* and *Acacia longifolia* correspond with that in the foliage leaves of a variety of species (of other genera) examined by Louis (1935).

A discussion of the morphology of the legume would be incomplete without consideration of the vascular anatomy. Saunders (1929) and Thompson (1929, 1931) have discussed it from points of view opposed to the monocarpellary interpretation of the legume. Eames (1931, with reference to the legume) and Arber (1933) discuss vascular anatomy and find in it support for the foliar nature of the carpel. These discussions are based on vasculation of the gynoecium at

relatively advanced stages. There is, therefore, nothing in this paper with which to contrast them. It is to be noted, however, that the relative positions of the primordium of the midrib, the extension of the pith and the suppressed apex, together with the later origin of the primordia of the marginal bundles appear in keeping with a foliar interpretation.

After considering the facts of ontogeny described in this paper, and discussing them in relation to facts and ideas put forward by other workers, I can see no reason for doubting that the legumes of *Acacia suaveolens* and *Acacia longifolia* are of foliar nature; rather does the evidence support that morphological interpretation.

The Flower.

The ascription of a foliar nature to the legume, that is, to the monocarpellary gynoecium of the Leguminosae, immediately raises the question of the morphology of the flower. Is it a modified leafy shoot? This question has been discussed by many recent workers from various points of view. I will only add certain comments which arise out of the present study.

The special contribution of this paper to the subject is the description of the meristematic activity of the floral apex with cellular detail, and the comparison thereof with the similar activity of at least some types of the vegetative apex. It has been seen that there is fundamentally no difference between them, except the limitation of growth of the floral axis. The appendages are initiated in the same manner on vegetative and floral apices. In the floral apices of the two *Acacia* species we have seen the limitation of growth by the failure of formation of the vacuolating dividing tissue which is the tissue responsible mainly for the production of node and internode (Priestly, 1929, p. 69). Priestly and Swingle (1929, p. 27) refer to the work of Koch (1893) in which he showed that "in practically all trees and shrubs the new lateral buds arise some time after the leaf initials have appeared at the growing point, at a time when the internodal development taking place makes these axillary meristematic groups distinct in origin from the meristematic tissue crowning the apex". With the absence of activity to form the internode, it is understandable that buds would be absent from the axils of floral appendages.

The considerations which arise out of the study of the histogenesis of the floral apices of *Acacia longifolia* and *Acacia suaveolens*, taken in comparison with accounts given by other workers of vegetative apices, cannot be regarded as contrary to, but as favourable to the interpretation of the flowers of these two species as modified leafy shoots.

SUMMARY AND CONCLUSION.

In some recent criticisms and modifications of the classical theory of the carpel as a modified leaf there is little presentation of evidence from primordial stages or with cellular detail. This paper studies both these aspects in *Acacia longifolia* and *Acacia suaveolens* in an attempt to find the relation of the carpel primordium to the apex of the floral axis.

There is a description of the relevant features of the species, the methods of manipulation of the material and the methods of examination including the construction of plasticene models from serial sections.

The evidence is first presented without use of the terms "apex", "legume", or "carpel".

The description of the external appearance of the development of the young flower records the formation of a "shoulder" on the apex after the formation of the petals. This "shoulder" is the seat of origin of the stamens and leaves a central "dome" which becomes slightly accentuated and gives rise to the ovule-bearing organ on one side of it.

The description of the internal appearance of the development of the young flower begins with the formation of the sepal initials and passes in close stages to the production of ovules. Particular attention is given to the distribution of the types of meristematic tissues and the vacuolated tissue. Three zones are recognized: fully meristematic, vacuolating dividing, and vacuolating extending, the first being the outer zone of from two to four layers.

The sepals and petals arise as folds in the outer layer under which divisions take place in the second layer with periclinal wall formation. The shoulder arises in the second layer by divisions with periclinal wall formation, the activity not extending over the central third of the longitudinal sectional contour and thus instituting the "dome". The stamens arise on the shoulder in the same manner as the sepals and the petals.

The enlargement of the "dome" is almost entirely by increase in cell size, spatial restriction causing the enlargement to express itself as increase in height.

The ovule-bearing organ arises laterally on this "dome" in the same manner as the sepals, petals and stamens arose, namely, by folding of the outer layer with divisions with periclinal wall-formation in the cells of the second layer, below the fold. The smallness of the "dome" causes the initial of the ovule-bearing organ to have a curved insertion. Restriction of space brings the primordium of the ovule-bearing organ into an erect position. Its early growth is by meristematic activity of the apex and margins. It assumes the form of a groove whose margins meet and, by differential growth of the inner and outer surfaces, enclose a cavity. Into this cavity the ovules grow from the edges of the arms of the groove. The assumption of the erect position by the organ brings the lower surface of the arms of the groove into close contact with the upper surface of the residue of the "dome".

The growth of the base of the ovule-bearing organ displaces the residue of the "dome", which finally appears to be but a part of the surface of the short stalk of the ovule-bearing organ. The tissues of the residue of the "dome" can be traced through the stages of development at least as far as the stage of the functional megaspore, by which time there is a strong tendency to the obliteration of the distinction between them and the adjacent tissues.

Apart from notice of the procambia of the ovule-bearing organ little notice is taken of the vascular tissues. The pith extends between the procambium of the midrib of the ovule-bearing organ and the residue of the "dome".

The foregoing description was made in terms of the histogenesis of an apical meristem giving rise to lateral organs. Such a description of floral ontogeny could not be found in the literature available to me here.

As a background for the interpretation of the evidence presented in this paper there is a discussion of recent work on the meristematic activity of the vegetative apices in the Angiosperms. Emphasis is laid on the response of the apex as a living entity to the mechanical influence of the formed lateral organs. The asymmetric distribution of meristematic activity is discussed in relation to the limitation of growth, and an argument advanced for the impossibility of an appendage being terminal in origin, so that there must always be a residue of the apex.

The evidence is interpreted as being compatible with all parts of the flowers of these two species being modified leaves. The legume arises laterally on the apex, the histology of whose suppression is observed. The legume is a single laminar structure growing in a manner similar to some vegetative leaves and bearing the ovules on its margins. The interpretation is illustrated by a series of models moulded according to measurements made of certain photomicrographs, and displayed in conjunction with those photomicrographs.

There is a discussion of the type of evidence necessary for a basis of morphological conclusions that imply some kind of ontogenetic process.

Bound up with recent theories of Saunders—Carpel Polymorphism—(1925 and 1929), Grégoire (1931), Thomas (1931 and 1934) and Thompson (1929, 1931, 1932 and 1934) are the following propositions: (1) the legume is a terminal structure; (2) the legume is not a single folded structure; (3) the legume is not a foliar structure.

After discussion, bearing in mind the evidence produced in this paper and comparing its nature with that of the evidence shown in support of the above propositions, it is concluded that: (1) the legume is a lateral structure; (2) the legume is a single, folded structure; (3) the evidence is compatible with the legume being a foliar structure (certainty on this point requires a wider study than that made in this paper).

The positive implications of the evidence are reviewed, with the conclusions that there is no reason for doubting that the legumes of *Acacia longifolia* and *Acacia suaveolens* are of foliar nature, and that it is reasonable to interpret the flowers of these species as modified leafy shoots.

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Notes on the Illustrations.

All the drawings were made with the aid of the camera lucida, the magnifications being determined by direct measurement.

All the preparations from which the photomicrographs were made were stained with Safranin, Orange G and Light Green (except with Haidenhain's Iron Alum Haematoxylin for Plate ii, fig. 3, and Plate v, figs. 60a, b), giving red nuclei, golden cytoplasm and green walls. The source of light was a Philips' Tungsten arc lamp. The light was passed through Wratten F (red) and density filters, and the source focussed on the back lens of the condenser by which it was focussed on the object. The cover glass correction collar on the objective (and sometimes the tube length) was adjusted for each photograph. On account of this the magnifications vary slightly, so that they have been given in round figures for the photomicrographs. Panchromatic plates were used. All figures in the plates are photomicrographs except the photographs of models shown in Plate v, figures 51-59, 61-65 and 71-75.

A few special annotations are indicated in the explanations of the figures. The following annotations have been standardized and apply in all cases:

ae, appressed epidermes; (arrow) $>$——→, the original centre of the upper surface of the axis, i.e., for the description (pp. 58-67) the original centre of the "dome", and for the interpretation (pp. 67-75) et seq., the original centre of the apex of the flower; *bG*, inner limit of the groove; *br*, bract; *G*, groove; *L*, for the description the ovule-bearing organ, for the interpretation, et seq., the legume; *mb*, marginal bundle (or its pro-cambium); *mr*, midrib (or its procambium); *ov*, ovule; *P*, pith; *pe*, petal; *se*, sepal; *sG*, surface of the groove; *st*, stamen.

EXPLANATION OF PLATES II-V.

Plate ii.—*Acacia longifolia.*

Photomicrographs of the whole or part of longitudinal sections of young flowers. Notice the distribution of the meristematic tissue. Magnification of all figures, × 240.

Fig. 1.—Shows sepals have arisen by cell division in second layer of the apex, under a fold in the outer layer.

Fig. 2.—Formation of the initials of the petals by cell division in the second layer of the apex, under a fold in the outer layer.

Figs. 3-5.—Stages in the formation of the "shoulder" (*sh*) by divisions with periclinal walls in the second layer of the apex except in the part represented by the central third of the sectional contour. The central part forms the "dome". Note the large-celled pith.

Figs. 6-8.—Origin of the initials of the stamens by cell divisions in the second layer under folds in the outer layer of the shoulder (*sh*). Variations in the shape of the apex (dome) and the axis. These figures are at slightly advancing stages. In 7, the section does not pass through any stamens on the right.

Figs. 9-13.—Progressive stages in the formation of the initial of the ovule-bearing organ (legume) on one side of the apex (dome) and by multiplication of the cells of the second layer with periclinal wall formation under a fold in the outer layer.

Figs. 14-18.—Development of the grooved structure of the primordium of the ovule-bearing organ (legume) which is forced into a vertical position by lack of space. The residue of the apex (dome) is displaced laterally and the arms of the groove extend above it, enclosing the original centre of the apex (dome). In 17 the section is slightly inclined to the plane of the groove and misses the midrib. (See Plate v, fig. 60*a, b,* for the next stage of *longifolia.*)

Plate iii.—*Acacia suaveolens.*

Photomicrographs of the whole or part of longitudinal sections of young flowers. Notice the distribution of the meristematic tissue. Magnifications of all figures, × 240.

Fig. 19.—Shows a sepal initial arising by cell division with periclinal wall formation in the second layer of the apex under a fold in the outer layer.

Fig. 20.—Shows initials of the petals formed by cell divisions in the second layer of the apex with periclinal wall formation, under a fold in the outer layer.

Figs. 21-23.—Stages in the formation of the "shoulder" (*sh*) by divisions with periclinal walls in the second layer of the apex, except in the part represented by the central third of the sectional contour. The central part forms the "dome". Stamen initials are already forming at the end of this process. The section for 22 is slightly displaced from the centre. Note the large-celled pith with the beginning of deposition of deeply-staining granules, which in the figures frequently appear as brightly shining bodies (red stain, red filter, panchromatic plates).

Figs. 24-27.—Origin of the initials of the stamens in the second layer of the "shoulder" (*sh*) under folds in the outer layer. 25-27 show the regularity of the layers of the apex (dome), although there has been distortion by external pressure in the cases of 25 and 26. In this species the dome is defined later than in *longifolia,* cf. figure 24 with figure 6 on Plate ii. In 26 the section does not pass through any stamens on the right.

Figs. 28-31.—Progressive stages in the formation of the initial of the ovule-bearing organ (legume) on one side of the apex (dome), by multiplication of the cells of the second layer with periclinal wall formation under a fold in the outer layer.

Fig. 32.—Section passes down the groove which is becoming pronounced. The groove is wider than in *longifolia* and requires more than one section to show its extent. Stage of development is about that of *longifolia* shown in Plate ii, figure 15. Displaced tissue is lying above the darkly staining cells of the pith.

Plate iv.
Figs. 33*a* to 38*f.*—*Acacia suaveolens.* Magnification, × 240.

Showing the grooved nature of the young ovule-bearing organ (legume) which is forced into a vertical position by lack of space. The residue of the apex (dome) is displaced laterally and the arms of the groove extend above it enclosing the original centre. Notice the distribution of the meristematic tissue.

Figs. 33*a, b.*—Two sections in a longitudinal plane inclined to the plane of the groove, so that 33*b* includes the edge of the base of one side of the groove. The inclination to the plane of the groove makes the slope of the residual apex appear less steep. These are the two outside of three consecutive sections. Age younger than that of stage shown in Plate iii, figure 32.

Figs. 34*a, b.*—Two longitudinal sections down the groove; they are the outside ones of four consecutive sections, 34*b* is encroaching on the arm of the groove. Older stage than 32.

Figs. 35, 36.—Two longitudinal sections down the groove; they are the outside ones of three consecutive sections. 36 includes the face of the groove. Older stage than 34*a, b.*

Fig. 37.—Longitudinal section down the groove and including one face of it. Older stage than 35, 36 and than the stage of *longifolia* shown in Plate ii, figure 18. Note the great increase in cell size compared with figures 35, 36.

Figs. 38*a-f.*—Transverse sections of a young ovule-bearing organ (legume) about the stage of figures 34*a, b.* The series represents twelve sections at 6*μ,* beginning at the tip, of which Nos. 1, 4, 6, 8, 10 and 12 are shown. Though the midrib is indicated in *d* and *e,* it has scarcely been initiated yet. Detailed comparison of this series with figures 34*a, b,* will show the correspondence of the distribution of the meristematic and

vacuolating tissues. (The two organs appear reversed in aspect in these illustrations.) Note that the organ is grooved to the apex.

Figs. 39a-f.—*Acacia longifolia*.   Magnification, × 240.

Transverse sections of a young ovule-bearing organ of about the stage of Plate ii, figure 14. The series represents ten sections at 6μ, beginning at the tip, of which Nos. 1, 3, 5, 6, 8 and 10 are shown. This series is of a stage younger than that shown for *suaveolens*. Comparison of this series with Plate ii, figure 14, will show the correspondence of tissues. (Organs reversed in aspect.)

Figs. 40-50.—*Acacia suaveolens*.   Magnification, × 120.

Progressive and serial longitudinal sections of the central upper portion of the floral axis with the whole or part of the ovule-bearing organ (legume), showing the organ assuming an apparently terminal position with the lateral displacement, and suppression of the residue of the apex (dome), and the approach to obliteration of the boundaries between the upper part of the apex (dome) and the lower part of the arms of the groove, i.e., the lamina of the ovule-bearing organ (legume).

Figs. 40-41.—Consecutive sections showing the ovule primordia on the margin of one of the arms of the groove, and the demarcation between the lower part of the arm and upper part of the residue of the apex (dome). Same stage as Text-figure 13.

Fig. 42.—At the stage of the megasporogenous cell. Section is not truly vertical, hence the demarcation between the arm of the ovule-bearing organ (legume) and the upper part of the residue of the apex (dome) is not clear. It can be traced by the large cells of the hypodermis.

Figs. 43-6.—Consecutive sections at the stage of megaspore formation. The plane of section is not quite parallel with the plane of the groove. The maximum demarcation between the arms of the ovule-bearing organ (legume) and the residue of the apex (dome) would be underneath the junction of the arms. On account of the inclination of the plane of section, the four sections are needed to show the entirety of this line of maximum demarcation which can be followed from left to right in passing from figure 43 to 46. Away from this line there is some interpenetration of the cells of the two epidermes. The junction of these epidermes is shown in figure 43 by a dotted line. Note the extension of the dark staining deposition in the pith cells between the midrib and the residue of the apex (dome), and the bands of thickening on some of them.

Figs. 47-50.—Consecutive sections at the stage of the functional megaspore. As figures 43-46, except that the aspect is reversed and the line of demarcation is more easily traced by the more prominent hypodermis. Note the bands of thickening on some of the outer cells of the pith. By this stage it is only possible to identify the residue of the apex (dome) because of having traced it from the beginning.

Plate v.

Figs. 51-57.—Models of part of young flowers of *Acacia suaveolens* to show the development of the shoulder (*sh*) and the "dome" and the origin of the ovule-bearing organ from one side of the "dome". The explanation is in the text. The black dot is at the original centre of the apex (dome). All the stamens have been cut off in 56 and the central ones in 55 and 57. Except in 51, the petals have been cut off below the level of the stamens. The cards bearing the numbers have a width representing 50μ.

Figs. 58-9.—Models of part of young flowers of *Acacia longifolia*, showing the shoulder (*sh*), the "dome" and the young lateral ovule-bearing organ. Stamens have been cut off from the centre of 58. Black dot the original centre of the apex (dome). Explanation in the text. The cards bearing the numbers have a width representing 50μ.

Figs. 60a, b.—Consecutive longitudinal sections of a young ovule-bearing organ of *Acacia longifolia* at a stage just before the formation of ovule primordia. Shows the displacement of the residue of the apex (dome). The section is slightly inclined to the vertical. The line of demarcation between the lower part of the arm of the ovule-bearing organ (legume) and the upper part of the residue of the apex (dome) is still clearly discernible. The deeply staining deposition in the cells of the pith extends between the midrib and the residue of the apex (dome). Magnification, × 150.

Figs. 61-5.—Models showing the relation of the legume to the suppressed apex of *Acacia suaveolens*. White plasticene was used to represent the apex and grey plasticene to represent the legume. The models were made from measurements of illustrations as follows: 61 from Plate iii, fig. 27; 62 from Plate iii, fig. 30; 63 from Plate iii, fig. 31; 64 from Plate iv, figs. 35 and 36; and 65 from Plate iv, figs. 40 and 41, and Text-fig. 13.

Black dot represents the original centre of the apex.   Explanation in text; see also Figs. 71-75 on this Plate.   Magnification, × 96.

Figs. 66-8.—Longitudinal sections of young flowers of *Acacia suaveolens*, showing the regularity of the zonation of the tissues in spite of the distortion by the various compressions due to the pressure of the bracts and adjacent flowers (*fl*).   These are photographs respectively of flowers 1, 2 and 3 in Text-figure 11, but not all from the same section.   Magnification, × 150.

Figs. 69*a*-70.—Longitudinal sections of the ovule-bearing organ (legume) perpendicular to the plane of the groove and through the appressed margins, showing the appressed epidermes and portion of the upper part of the axis.   69*a*, of *Acacia suaveolens*, is at the same stage as Text-figure 13 and passes through the region about where the marginal bundles will form.   69*b* is of a similar stage of the same species as 69*a*, but the margins have not completely closed together, so that ovule primordia are exposed; a filament has been partly inserted into the open base of the organ.   70 is of *Acacia longifolia* at a stage slightly older than shown in Text-figure 6.   Magnifications, × 120.

Figs. 71-75.—Correspond with 61-65 of *Acacia suaveolens*.   The models are cut down longitudinally, the two halves of each opened out to show the disposition of the apex and legume in progressive stages of development.   With each opened model is placed a copy of the photomicrograph from the measurements of which it was constructed.   The photographs of the models have been brought to the same magnification as the photomicrographs.   For the correspondence of the models and photomicrographs see the explanation of figures 61-65 on this Plate.   A careful comparison of the distribution of the white (apex) and grey (legume) in the opened models with the cellular arrangement in the associated photomicrographs will demonstrate clearly the interpretation of the legume as lateral on a suppressed apex.   The photomicrograph in 75 was reversed (cf. Plate iv, fig. 41) for ease of comparison.   Magnification, × 240 for 71-4, and × 120 for 75.

Figs. 76-78.—Transverse sections of the ovule-bearing organ (legume) showing the appressed epidermes of the incurved margins.   76 is of *Acacia longifolia*, and is a photomicrograph of the section shown in Text-figure 10*b*.   77 is of *Acacia suaveolens* and is of a section of the base of the loculus of the ovule-bearing organ (legume) figured in Text-figure 15.   78 is of *Acacia longifolia* at about the time of fertilization, when the appressed epidermes of the incurved margins are still clearly to be seen. Magnifications, × 120.

Postscript, added 22nd April, 1936.

After I had completed the foregoing paper, Professor V. Grégoire kindly sent me a reprint of a recent paper of his (Grégoire, 1935*c*) in which he shows cellular detail in illustrations of the floral apex of *Ranunculus scleratus* and the vegetative apex of *Lonicera periclymenon*.   He points out (p. 299) that whereas the vegetative cone has a tunic enveloping a corpus furnished with an initial region that can cause elongation in growth, the floral summit has only a meristematic cloak ("Manchon") covering a mass of parenchyma and cannot grow in length.   Discussing certain abnormalities in flowering described by Brieger (1935) in *Primula*, he attributes the presence or absence of sepals in different forms of proliferation to the difference in meristematic organization between vegetative and floral apices.   Sepals are developed by the organization of a vegetative apex, from which there is a transition to the floral type of apex by the time of formation of the initials of the petals.   It seems to me that the differences described by Grégoire are of a similar kind to those that I have described and attributed to limitation of growth.

Finality in the interpretation of the flower will only be attained after very wide inquiry.   In the meanwhile, it is well to emphasize that the classical interpretation is that the carpel is a *modified* fertile leaf and the flower a *modified* leafy shoot.   A different appearance in the meristematic organization of the two forms of apex should, therefore, not be regarded as necessarily antagonistic to that interpretation.